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Differences between Leg and Flight Muscle of the Giant Water Bug, Lethocerus americanus [1, 2]

By JOHN W. KENNEY and A. GLENN RICHARDS, Department of Entomology and Economic Zoology, University of Minnesota

In a comparative study of enzyme activity in muscle of several animals, Davison and Richards (1) reported activation energies of 8,500, 15,000, and 20,000 calories per mole for the apyrase (ATPase) enzyme system from muscle of minnow, crayfish, and cockroach, respectively. Various morphological and physiological differences between vertebrate and invertebrate muscle are well known. In addition, differences between different muscles of an individual may be seen in serial section of numerous insects. Recently, Edwards *et al.* (2), using an electron microscope, have described differences in the ultrastructure of flight and coxal muscles of the beetle *Hydrophilus piceus*. The possibility of finding physiological differences correlated with the morphological differences between muscle systems for any one species seems worthy of consideration. Some work in this direction has recently been published by Gilmour and Calaby (3, 4). Using desert locusts, they found that the enzymes myokinase, calcium-activated apyrase, and myosin-ATPase were similar in activity level in leg and flight muscle, but that inorganic pyrophosphatase and magnesium-activated apyrase were

[1] Paper No. 3235, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota.

[2] The work presented here was performed under terms of a contract between the Office of the Surgeon General, U. S. Army, and the University of Minnesota.

2–3 × more active in crude extracts of flight muscle. Since the activity of the apyrase enzyme system in breaking down adenosine triphosphate (ATP) is thought to supply the energy for muscle contraction, this enzyme was chosen for assay of its activity in homogenates of leg and flight muscle.

Male giant water bugs were collected under mercury vapor lamps at gasoline stations in a marshy, rural region near St. Paul, Minnesota. Femoral muscle and dorsal longitudinal flight muscle were used. Histological examination was made of fresh muscle teased in physiological saline solution. For enzyme assays, muscle was dissected out in physiological saline solution at 0° C., blotted, weighed on an analytical balance, and homogenized in glass in ice-cold distilled water. The amount of distilled water used was adjusted so that, on the basis of wet weight of tissue, the homogenates always contained 3.64 milligrams per 0.04 milliliter, *i.e.*, 3.64 mg. per reaction vessel. Subsequent protein nitrogen determinations by micro-Kjeldahl on aliquots of the several homogenate preparations showed 5.7–6.8 micrograms of nitrogen (average 6.3) per 0.04 ml. of homogenate for leg muscle, and 7.5–13.6 micrograms (average 10.0) per 0.04 ml. of homogenate for flight muscle.

The substrate mixture for enzyme activity determinations contained 0.2 ml. of 0.02 molar sodium ATP (Nutritional Biochemicals Co.), 0.2 ml. of 0.2 molar $MgCl_2$, and 1.56 ml. of Sigma 7–9 buffer at pH 7.8. The buffer solution was made by adjusting 0.3 molar Sigma 7–9 solution to pH 7.8 by titrating with 0.1 molar HCl.

Four hundredths of a milliliter of homogenate were added to the substrate mixture to bring the final reaction volume to 2 ml. Five minutes were allowed for temperature equilibration of the reaction vessels and substrate mixture before addition of the homogenate. The reaction was started by the addition of the homogenate to the substrate mixture, and was stopped five minutes later by the addition of 2 ml. of 10% trichloracetic acid solution. Temperature control was according to Steinbach (6), and phosphate was determined by the well known method of Fiske and Subbarow. Controls were routinely run for inorganic phosphate initially present. Preliminary tests showed that experiments with various amounts of homogenate, plotted against activity in unit time, gave a series of points falling on a straight line which on prolongation passed through the zero intercept.

Histologically the leg and flight muscle of *Lethocerus* are quite different in appearance *in vivo*. The leg muscle is clear

and hyaline, on gentle teasing in saline solution it gives large fibers (350–400 μ in diameter) which with polarized light exhibit strong birefringence and alternating isotropic and anisotropic bands, it also has a distinct sarcolemma (sheath), and on homogenization it gives a clear suspension. In contrast, the flight muscle is opaque and orangish-red, on gentle teasing it gives smaller fibers (75 μ) which with polarized light show only moderate birefringence (perhaps due to scattering and absorption of much of the light) and no clear banding, it shows no sarcolemma, and on homogenization it gives an opaque milky suspension. Also, on dissection one sees bands of tracheae (*ca* 100 μ diameter) wrapped around the large bundles of flight muscle giving the appearance of transverse scale-like striations; no such tracheal investment is found around the leg muscles. Except for fiber diameters, these differences seem similar to those reported by Edwards *et al.* (2) for the beetle *Hydrophilus*.

The data from enzyme assays at various temperatures are plotted in Figure 1 where each point usually represents a single determination. The data are plotted both on the basis of activity per unit of protein nitrogen (curves *A* and *B*) and on the basis of activity per unit of wet tissue weight (curves *C* and *D*). Several differences between leg and flight muscle are evident. First, and most obviously, the leg muscle showed considerably more activity at any temperature throughout the viable range. Second, the flight muscle gave a series of points that fit reasonably well on a straight line from 0 to 40° C. whereas leg muscle gave a series of points fitting either the arc of a circle (as drawn in curve *A*) or two straight lines (as drawn for curve *C*). And, third, leg muscle was thermally inactivated at higher temperatures more abruptly than flight muscle (curves *A* and *C* fall more precipitously above 45° C.).

Through the range 0–20° C., the leg muscle showed about 2.2 × as much activity on the basis of wet weight, and about 3.25 × as much activity on the basis of nitrogen content of the tissue. Above 20° C. the difference decreases. It is interesting to note that these differences are the opposite of those recorded by Gilmour and Calaby for desert locusts. Presumably our

data can be compared with data from their "Mg-activated apyrase of crude extracts." They record 2–3 × (4) or 2–5 × (3) as much activity from flight muscle as from leg muscle of locusts. It does not seem likely that the differences in technique could account for such opposite ratios. It seems more likely that the differences are real, *i.e.*, that leg muscle does hydrolyze more ATP in the water bug whereas flight muscle is more active in the locust. Determinations on more species will be required before warranting attempts to correlate such differences with the relative importance of various muscle sets in different species of insects.

With the second point, namely the straight lines of curves *B* and *D* versus the curved or bent lines of curves *A* and *C*, we encounter one of the usually unsatisfactory aspects of fitting curves to sets of experimentally determined points. One can objectively fit a regression line to any series of points by the method of least squares, as has been done here for curves *B–D*. But one usually has to decide subjectively whether the points fall adequately close to a straight line (since there is obvious inactivation of the enzyme system at high temperatures). In the present case a check is provided by the fact that activity was determined both in relation to tissue wet weight and to tissue nitrogen, and the tissue nitrogen value is different for the two tissues. The difference *in spacing* between curves *A–B* and curves *C–D* should be the same as the determined difference in tissue nitrogen, *i.e.*, curves *A–B* should be approximately 1.6 × as far apart as curves *C–D*. But one finds on fitting regression lines that curves *A–B* are only 1.35 × as far apart as *C–D* if one uses all points from 0 to 40° C., but that they are 1.5 × if only the points from 0 to 20° C. are considered. This gives justification to saying that, whereas the values for flight muscle appear adequately fitted by a straight line over the range 0–40° C., the values for leg muscle can be adequately fitted by a single straight line only over the range 0–20° C. (otherwise stated, the high points above the center of the single regression line drawn in curve *A* are not due to analytical error but represent deviation of the curve above these temperatures). One can, then, either

fit an arc to the values from leg muscle, as done in curve *A*, or fit a straight line to the values from 0 to 20° C. and another straight line for the range 20–40°, as done in curve *C* (the two straight lines being approximately parallel to tangents of the

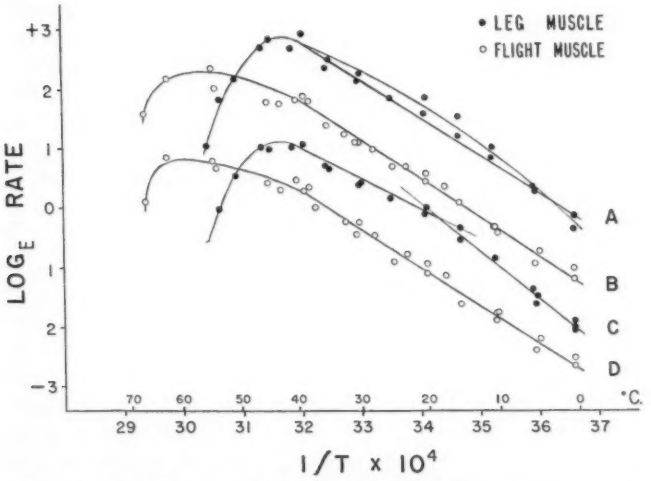

FIG. 1. Arrhenius type plot of apyrase (ATPase) enzyme activity as a function of temperature. Values on the abscissa are the reciprocals of absolute temperature, with the corresponding centigrade degrees given above the line for convenience. Values on the ordinate are the log$_e$ of values for rate of hydrolysis of adenosine triphosphate (ATP); for curves *A* and *B* this is log$_e$ (μg. P/mg. N/min.) $\times 10^{-1}$, for curves *C* and *D* this is log$_e$ (μg. P/mg. tissue/min.) $\times 10$.

The straight lines between 0 and 40° C. in curves *A*, *B*, and *D* and the straight line between 0 and 20° C. in curve *C* are regression lines fitted by the method of least squares. The arc in curve *A* and the lines above 40° C. were fitted visually.

arc in curve *A* at 10° and 30°, respectively). Whichever way is done, the difference in spacing has fallen to 1.3 × at 35° C., *i.e.*, the leg muscle is clearly exhibiting a greater deleterious effect from the high temperature, an effect which becomes even more marked in the precipitous fall of curves *A* and *C* in the range 45–55° C.

Using the Arrhenius equation:

$$k_2 = k_1 \cdot e^{\frac{\mu}{2}\left(\frac{1}{T_1}-\frac{1}{T_2}\right)},$$

one can calculate the μ value or so-called activation energy.[3] This is an expression of the slope of the lines drawn in Figure 1. The steeper the line, the higher the μ value, and the greater amount of effect temperature has on the rate of the reaction. Flight muscle of *Lethocerus* shows a μ value of about 13,000. Leg muscle gives a value of 16,000 in the range 0–20° C., the value calculable at 30° C. (if valid) being about 10,000. These values are distinctly lower than the value of 20,000 reported for cockroach muscle (1) and the value of 29,600 reported for locust muscle (5). Whether this lower value can be related, as Davison and Richards have suggested (1), to the fact that *Lethocerus* is inactivated only at lower temperatures remains for further comparative work to determine. It is, however, of interest to record that male *Lethocerus* are completely inactivated at 0° C., will try to walk at 2° C., and swim feebly at 4° C., but that we were unable to induce them to fly at temperatures below 10° C. At 10° C. the absolute activity of the apyrase enzyme per milligram of flight muscle is similar to that of leg muscle near 0° C. (Fig. 1). Perhaps there is a certain minimal amount of apyrase activity per milligram of tissue for

[3] The symbols k_1 and k_2 represent the measured activity rates at temperatures T_1 and T_2 (absolute temp. scale), e is the base of natural logarithms, and μ is the symbol for which one solves the equation. If one reads values from Figure 1, the equation can conveniently be rewritten as:

$$\log_e k_2 - \log_e k_1 = \frac{\mu}{2}\left(\frac{1}{T_1} - \frac{1}{T_2}\right)$$

or

$$\mu = \frac{2\,(\log_e k_2 - \log_e k_1)}{(1/T_1) - (1/T_2)}.$$

Thus, reading values from curve B at 21° and 30° C.,

$$\mu = \frac{2\,(1.14 - 0.48)}{0.0034 - 0.0033} = \frac{1.32}{0.0001} = 13{,}200,$$ the units being cal./mole.

muscle contraction, but, if so, then preliminary tests we have run on other species of insects indicate that the absolute activity necessary is different in different species.

Incidentally, Gilmour and Calaby (5) have suggested that the high degree of dependence of wing rate on temperature in insects is related to and perhaps due to the high activation energies of flight muscle apyrase. They call this a biochemical explanation of the biological phenomenon. But, although the value of 29,600 recorded by them for desert locusts is indeed high, the value of 13,000 found for *Lethocerus* flight muscle is within the range (8,000–17,000) of most other biological processes that have been measured (7).

The identity and characterization of enzymes which split phosphorus from ATP is in a confused state. Some authors use the terms "apyrase" and "ATPase" interchangeably, other authors speak of them as distinct entities. One gathers from the recent papers of Gilmour and Calaby (3, 4) that the enzyme picture in insect muscle is so complex that specific names for the components cannot be satisfactorily assigned at the present time. The point of view common among biochemists is that data from homogenates (which are very complex mixtures) cannot be interpreted until all the components have been isolated and characterized. This may well be true. Whole homogenates do seem inadequate for assessing the differences between the curves for leg and flight muscle. Conceivably, the same "Mg-activated apyrase" may be present in both, most of the quantitative differences being due to corresponding differences in concentration of this enzyme, and the qualitative differences (shape of curves) due to other components. Such questions do require studies on fractionated homogenates. But whole homogenates contain the components of the living system and are quite sufficient to show that leg and flight muscles of *Lethocerus* are both qualitatively and quantitatively different in hydrolyzing ATP, and further that the quantitative differences in *Lethocerus* are opposite to those recorded for locusts (*Locusta* and *Gastrimargus*).

Sumarizing, flight and leg muscles of the giant water bug are quite different in color, gross histology, protein content, and both

quantitative and qualitative aspects of apyrase enzyme activity. The leg muscle has 2–3 × as much apyrase activity but lacks readily visible amounts of the reddish muscle pigments and has only 60% as much protein nitrogen. Probably the flight muscles are inactivated by cold at a higher temperature than leg muscles are in this species. Clearly, these muscle sets are different from one another, and, equally clearly, the relative enzyme activity rates in this bug do not parallel those reported by Gilmour and Calaby for desert locusts.

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A Preliminary Report on the Chilopoda of Missouri

By RALPH E. CRABILL, JR., Department of Biology, Saint Louis University

The present discussion is based upon a collection of centipedes captured in St. Louis County, Missouri, chiefly in a locality that has informally been designated "Ranken" [1] by local naturalists.

These specimens were generously placed in my hands by Dr. E. P. Meiners, a local physician and naturalist whose enthusiasm for natural history in general and whose large, beautifully or-

[1] Ranken, a tract of land, part of which is occupied today by the Beaumont Boy Scout Reservation, still reflects here and there an almost primeval Ozarkian nature, even though it is already experiencing the effects of expanding civilization. Situated on U. S. Highway 66, it is some twenty-three miles west of St. Louis, about five miles west of Valley Park and two miles east of Eureka.

dered insect collection and extensive entomological library are well known to many persons in this area. I am deeply indebted to Dr. Meiners for the opportunity of being able to study his carefully preserved centipede collection.

GEOPHILOMORPHA

Geophilidae

Geophilus vittatus (Rafinesque). This ubiquitous species, formerly known as *Geophilus rubens* Say,[2] has been reported to occur from Massachusetts west to Nebraska and eastern Texas, and south to the Gulf states. A single male with 51 pairs of legs was taken at Ranken.

Geophilus mordax Meinert [*sensu stricto*]. Three males each with 53 pairs of legs; two females with 55, one female with 57 pairs of legs. All six specimens possess heavily sclerotized, consolidated paxilli and sacculi, and the ventral coxopleural pores of all are concentrated under or adjacent to the ultimate pedal sternite. In addition, the coxopleuron of each shows the peculiar pigmented thickening which represents a closed ventroposterior pore. The significance of these characters in the light of the true identify of *mordax* has recently been discussed elsewhere.[3]

Arenophilus watsingus Chamberlin. In Meiners' series of eleven specimens the following leg-pair distribution was recorded. Females: 57 pairs, 3; 59 pairs, 2; 61 pairs, 2. Males: 55 pairs, 1; 57 pairs, 2; 59 pairs, 1. The species reportedly ranges from Virginia, Kentucky, and Missouri south to the Gulf states. Although the closely-related *bipuncticeps* was not collected at Ranken by Dr. Meiners, one specimen was taken at Glencoe, St. Louis county, by Brother Charles Roe of the Christian Brothers College.

Pachymerium ferrugineum (C. L. Koch). This well-known European form is common to many localities in this country into which it has apparently been introduced. Both in Europe and in the United States it seems to prefer moist, sandy

[2] CRABILL, Florida Entomologist, XXXVI (2), p. 78, (1953).
[3] CRABILL, Proc. Ent. Soc. Washington, LVI, pp. 182–187, (1954).

situations in the vicinity of water. The Ranken specimens agree in all particulars with New York State and German representatives.

Arctogeophilus fulvus (Wood). A single female with 55 pairs of legs. This long neglected, handsome centipede is now known from Philadelphia, Pennsylvania, from Big Knob Hill, and Crab Tree Corners, Virginia, and from the present locality. Dr. Meiners' only female has 55 pairs of legs and compares favorably with those captured in Virginia by R. L. Hoffman.

Dignathodontidae

Strigamia bidens Wood. A male with 69 and a female with 71 pairs of legs were captured at Ranken; both compare favorably with eastern specimens. The species is now believed to range from eastern Pennsylvania south to northern Georgia and Louisiana, and west to eastern Missouri.

Strigamia bothriopa Wood. One female with 49 pairs of legs. Because this species has been confused with *S. fulva* Sager for many years, one cannot rely upon previously published distributional records. However, in the light of specimens personally examined, I should guess *bothriopa* to occur throughout the midwest and east perhaps as far south as the Gulf states.

Schendylidae

Escaryus missouriensis Chamberlin. This striking form is now represented by three specimens: a male holotype from St. Louis county, Missouri (4.3 miles northwest of Glencoe), with 59 pairs of legs; a female from Dallon's Spring Cave, Indiana, with 57 pairs of legs; and the present male from Ranken, with 59 pairs of legs. The most recently discovered male, 73 mm. long, is thus larger than either of the two previously known specimens. Also its controversial telopodital lappets are quite long. In general it is very similar to the Indiana female recently described.[4]

[4] CRABILL, Journ. New York Ent. Soc., LXI, p. 96, (1953).

SCOLOPENDROMORPHA

Scolopendridae

Cormocephalus (Hemiscolopendra) punctiventris (Newport). This species appears to range from coastal Massachusetts south to the Gulf states and north to southeastern Nebraska. I also have seen specimens from Arizona, its westernmost outpost so far as I am aware. Ranken yielded one specimen.

Cryptopidae

Cryptops hortensis Leach. The common European *hortensis* has only recently been shown to inhabit parts of the United States into which it has probably been introduced. It is now known only from Ithaca and the Bronx, New York, from Salt Lake City, Utah, and from the present area. One specimen was captured.

Theatops spinicaudus (Wood). Western Pennsylvania south to the Gulf coast, west to Missouri and Arkansas. No specimens referable to Say's *posticus* were taken at Ranken. The Say species seems to be more prevalent than *spinicaudus* in the southeastern United States.

Scolopocryptops rubiginosus Koch [formerly *Otocryptops*[5]]. These specimens are provisionally referred to the Koch species, but complete assurance of their true identity must await the evidence of further extensive collecting in this and in neighboring areas to the northwest. Whereas typical *rubiginosus* specimens, seen from Kansas, Nebraska, Iowa, and Korea, all possess strong, complete paramedian sutures at least on tergites (4–6) through 20, the Ranken forms show marked variation particularly in this character. Some have complete though weak paramedian sutures on tergites 6 through 17, and others have many or even all of the paramedian sutures very narrowly broken in the middle. These specimens could not be confused with typical eastern representatives of the closely related *sexspinosus*, in which I have never found more than extremely short sutural fragments anteriorly and posteriorly on any given

[5] CRABILL, Ent. News, LXIV, p. 96, (1953).

tergite. Thus, the Ranken specimens seem to occupy an intermediate position between the typically eastern *sexspinosus* and the northcentral *rubiginosus*. (Each has been reported from eastern Asia.) This evidence seems to me to be sufficient at least to raise the question of whether *rubiginosus* and *sexspinosus* are geographical races (subspecies) of one far-flung polytypic species. And if the future proves this to be the case, then our ideas concerning the constitution of the entire genus will stand in need of review.

LITHOBIOMORPHA

Ethopolyinae

Bothropolys multidentatus (Newport). East of the Mississippi *multidentatus* is probably the most widespread endemic lithobiid. Particularly common under tree bark, where conditions are unvaryingly on the moist side, this form is evidently not especially inhibited in its dispersal by limited temperature variations. It does definitely seem to be sensitive to variations in environmental moisture. Thus I have found it to be as common in Ithaca, New York, as in Virginia or the Carolinas. The Missouri specimens that I have seen (from Jefferson City and St. Louis county) do not appear to differ significantly from the thousands of eastern representatives that I have examined.

Lithobiinae

Sozibius proridens (Bollman). The original orthography of the trivial name seems to be *proridens* rather than *providens* as cited in 1922 by Chamberlin.[6] The species is known to range from extreme southeastern New York State south and west to Mississippi, Arkansas, and Missouri. It is the least common lithobiid in the Ranken collection.

Pokabius bilabiatus verdescens (Chamberlin). The few Ranken specimens are provisionally referred to the Chamberlin subspecies. Although all lack spur VTrM on the 13th leg, an unstable VTrM has been found in several other North Ameri-

[6] CHAMBERLIN, Bull. Mus. Comp. Zool. Harv., LVII, p. 268, (1922).

can lithobiids. In fact, in certain species this type of variability may be seen to occur within a relatively small population. In the original description Chamberlin says [7] that the two subspecies "occur in the same general region." It is thus not unlikely that the criteria used for distinguishing these subspecies are actually manifestations of a highly variable species and that the two forms are non-genetically fixed variants. *P. bilabiatus* is presently known to range from Ohio west to Nebraska and Kansas, south to Louisiana, and north to Minnesota.

Neolithobius voracior (Chamberlin). This is by far the commonest lithobiid taken at Ranken and in nearby St. Louis county localities. It is evidently also very prevalent at Jefferson City from which I have seen many specimens. Elsewhere *voracior* is know from Illinois and Mississippi.

Nadabius iowensis (Meinert). This widespread, typically midwestern form reportedly ranges from Idaho east to Ohio and south to Tennessee. It is very common at Ranken.

Nadabius ameles Chamberlin. Elsewhere the species has been reported from Mineral Springs, Indiana (type locality), and from Chicago, Illinois. I have found specimens that seem to agree with the original description from several localities in Connecticut and most recently from eastern Missouri.

SCUTIGEROMORPHA

Scutigeridae

Scutigera coleoptrata (Linné). One large female was captured outside at Ranken. The common "house centipede," while rarely encountered out of doors in the northeast, has been found to forsake human dwellings commonly in warmer parts of the country.

[7] CHAMBERLIN, Bull. Mus. Comp. Zool. Harvard, LVII, p. 353, (1922).

The Earwigs Euborellia cincticollis and E. annulipes in Arizona

In Hebard's 1935 list of the Dermaptera and Orthoptera of Arizona the only earwigs recorded from the state are *Spongovostox apicedentatus* (Caud.) and *Doru lineare* (Esch.), and we are unaware of any later records. Two other species from Arizona are contained in the Wallace collection, now on deposit in the University of Michigan Museum of Zoology. One of these, *Euborellia cincticollis* (Gerst.), is an African species recorded as established in the United States by Gurney in 1950.[1] His specimens were taken at four localities in the lower valley of the Colorado River in California between 1946 and 1949; all were winged and taken at lights. Wallace has collected 3 ♂, 6 ♀ of this species at Tempe, Maricopa Co., Arizona, July 4–Aug. 12, 1951, and a single ♀ July 25, 1952; D. E. Whitacre also took 2 ♀ at Tempe, July 24, 1951. These specimens, like Gurney's, are all fully winged and were all taken at lights. The second species, *Euborellia annulipes* (Lucas), is an apterous tropicopolitan form established in the southern states (west to southeastern Kansas and central Oklahoma and Texas) and in California, but not hitherto recorded from the arid southwest. The following material from Maricopa Co., Arizona, is contained in the Wallace collection: Tempe, Mar. 15, 1951, 1 juv. ♀ on irrigation dike; Tempe, Nov. 28, 1951, 1 ♀ in building; Scottsdale, Dec. 6, 1951, 1 ♂, 1 ♀ under bark of ocotilla, near roots, in irrigated land. Gurney is correct in saying that the ♂ of *cincticollis* is distinguished from that of *annulipes* by the slightly emarginate apex of the last sternite, but in *annulipes* this margin is normally subtruncate, not broadly convex as stated by Gurney. The penial differences between the two species which Gurney describes are not readily appreciable.

T. H. Hubbell and H. S. Wallace

[1] See also: Ting, P. C. 1951. An African earwig in California. Bull. Dept. Agr. Calif. 40: 4–9, ill.

The Ant Leptothorax muscorum (Nylander) in North America

By WILLIAM L. BROWN, JR., Museum of Comparative Zoology, Harvard University

The small ant *Leptothorax muscorum* (Nylander), of subfamily Myrmicinae, is one of the very few truly boreal-alpine members of its family. It is known from a very wide area in the northern Palearctic, and at least in the western part of Europe frequently occurs sympatrically with the similar but distinct species, *L. acervorum* (Fabricius).[1] The presence of true *L. muscorum* in North America has been indicated on several past occasions, but the tendency to treat the North American and Eurasian populations as separate taxonomically has grown stronger with each consideration of the problem. This tendency now appears to have been the result of several taxonomic accidents and the regrettable practice of North American taxonomists in refusing to consider populations outside their own continent. Unfortunately, the first man to consider fully the extra-continental relationships of the North American representative of the *muscorum* complex was deceived by a misleading set of circumstances.

In his recent book (*loc. cit. infra*), to which the reader is referred for extensive historical discussion, Creighton has separated as distinct species the Eurasian *L. muscorum* and *L. acervorum* and the Nearctic *L. canadensis* (Provancher), and has cited the characteristics of each. However, it has now been determined that Creighton depended for his characterization of European *L. muscorum* upon a set of specimens left grouped by W. M. Wheeler under that name, mostly from Swiss and German localities. This set now proves to be a mixture not only of *muscorum* and *acervorum,* but also of one or two super-

[1] I consider the current discussion of the application of the subgeneric names *Leptothorax s. str., Mychothorax* Ruzsky, and *Myrafant* M. R. Smith to be pointless. *Leptothorax* and *Mychothorax* are known to be isogenotypic synonyms; *Myrafant* is a subjective synonym of *Leptothorax* in view of the fact that the antennal segmentation, metanotal impression and radial cell characters will not hold for the entire world fauna of the genus. This question will be discussed in a separate paper.

ficially similar forms in the *tuberum-nylanderi* group; the sorting of this series reveals that Creighton probably drew most or all of his *muscorum* diagnosis from members of the last-named group.

The mixup in the Wheeler Collection often extended to single triple-mount pins, and anyone who has ever worked with this collection realizes how likely it is to deceive even the most careful of workers. The confusion was discovered only when a new addition to the collection was being made from the *Leptothorax* of the Palearctic Finzi Collection, containing pure series of the species in question determined by such authorities as Mayr, Emery, Menozzi, Müller and Finzi. The *muscorum* series from the Finzi Collection, as authentic as can be obtained, were compared with the various forms of the *L. canadensis* complex in the Museum of Comparative Zoology; the detailed correspondence of characters indicates that *muscorum* and *canadensis* are conspecific. In fact, many of the western North American samples are as similar to the European samples as allonidal specimens can be expected to become. The European series do show a tendency, or average trend, toward slightly finer, more attenuate dorsigastric pilosity than is shown by most American samples, but even in this character, certain western Nearctic nest series can be found to match, or even overreach, this Old World variation. All degrees of variation in this character occur in the western United States, usually on a strictly local basis, and it seems impossible to correlate its distribution with coloration or any other character known to vary geographically.

Eastern North American populations are usually distinguishable by means of their concolorous piceous or blackish pigmentation, supposed to mark the nominate race of *canadensis,* but this condition merges toward the west into the "typical *muscorum*" or "*calderoni*" type of variation, in which the alitrunk is a contrasting yellowish-ferruginous against the brown or piceous head and gaster. The gradualness of this east-west color shift has been somewhat obscured by the recognition of race *yankee,* embracing both color forms, but removed from consideration on

the basis of a sculptural distinction. The dark concoloration reappears at high altitudes in the Rockies and in the Arctic Northwest of Alaska and Canada, often in mixed series with bicolored forms. Bicolored individuals are by no means restricted to the West of North America, for nests taken on Mt. Washington, New Hampshire, within sight of the Atlantic Ocean, frequently contain a proportion of fully adult but bicolorous individuals. Color variation in Eurasia is not well known, but Dr. H. Kutter assures me that Swiss samples, while somewhat variable, are all bicolored. For me, this situation is readily interpreted as a circumpolar cline with numerous local reversals and irregularities.

After rightly synonymizing several variants, Creighton retained in addition to the nominate race of *canadensis* three North American races: *kincaidi* (Alaska, British Columbia, etc.), *calderoni* (northern California north into British Columbia and Alberta), and *yankee* (lower levels in the Rockies and Black Hills). The typical *canadensis* was assigned the territory to the east of these, and also the upper levels of the Rocky Mountains. Judging from his arrangement of the material in the Museum of Comparative Zoology as I found it, Creighton considered approximately half of the total Nearctic material to represent intergrades among the four races.

The additional racial characters cited are, at least for me, extremely difficult or impossible to pin down. The "suberect" short pilosity of the anterior scape surfaces, marking *kincaidi*, could be described equally well as "decumbent," so feebly does it diverge from the fully appressed position. At any rate, this kind of pilosity of the scapes occurs in specimens from Skagway, Alaska, and Olympia, Washington, considered to be *kincaidi* by Creighton, but it may also be found in series from remote localities (such as Mt. Washington). Surprisingly, the *kincaidi* types, from Metlakahtla, Alaska, appear to me to have the scape hairs as fully appressed as the majority of specimens placed to other races by Creighton! The character may vary only as an artifact of preservation, but in any case, it certainly does not mark exclusively and uniformly any northwestern Nearctic population so far as I can tell from the available material.

Race *yankee* is reserved for forms having the superimposed rugulation of the alitruncal (presumably chiefly the pronotal) dorsum reduced and indistinct. Samples more or less fitting this description can be found at certain lower-altitude stations in the Rockies and Black Hills, as Creighton claims, but other samples from the same or very close localities, so far as the data go, have the rugulation more or less developed. This character is a feeble one at best, and a most illusory one, subject to changes with the pigment and lighting arrangements, at the worst. Due to the gradational nature of the dorsal pronotal sculpture, almost any specimen might be considered transitional to other races. Another disturbing feature in the evidence for *yankee* is the paucity of precise and specific citation of the sculptural variation with altitude and latitude. In the case of such an elusive difference, precise and detailed documentation is surely required.

Considering all suspected or known geographically variable characters of *muscorum* in North America together, we may stress: (1) their extreme elusiveness, (2) notable exceptions to and reversals of their supposed geographical exclusiveness, (3) the breadth of their intergradation, and (4) their lack of geographic concordance. I believe that it may accurately be stated that from no racial division so far proposed for this species can any satisfactory general idea of the full distribution of any or all of the variable characters be gained. If, as is generally claimed, the function of the racial category is the description in symbolic terms of geographical variation and/or the indication of probable potential incipient species, then I would say that formal racial subdivision certainly falls far short of the ideal in this particular case. In this connection, see Wilson and Brown, 1953.

I prefer at this time to emphasize the species-unity of the populations discussed by formally synonymizing all the North American racial names under *L. muscorum*. Decisions as to possible formalised subdivisions should be left to a future study of the trends and details of geographical variation backed by the necessary fullness of data, so far lacking from all published references to this species. For fuller references to the new

synonyms listed below, and for further synonymy, type localities, and other information, see Creighton (1950) and also the Genera Insectorum listings of Emery (1922). I am unfamiliar with the variants and possible synonyms of *L. muscorum* described from Eurasia, chiefly by Ruzsky, and cannot discuss them here in the absence of relevant material. I can, however, confirm the previous synonymization of var. *gredleri* Mayr on the basis of a specimen determined as *gredleri* by Mayr himself, now in the Museum of Comparative Zoology.

Leptothorax muscorum (Nylander)

Myrmica muscorum Nylander, 1846, Acta Soc. Sci. Fenn., 2: 1054, worker, female, male; *nec Leptothorax* (*Mychothorax*) *muscorum* of Creighton, 1950, pp. 274–275.

Leptothorax Canadensis Provancher, 1887, Addit. Correct. Faune Ent. Canad. Hym., Quebec, p. 245, worker, female, male; *L.* (*M.*) *canadensis,* Creighton, 1950, pp. 274–276. New synonymy.

Leptothorax (*Mychothorax*) *acervorum canadensis* var. *calderoni* Forel, 1914, Deutsch. ent. Zeitschr., p. 617, worker, female; *L.* (*M.*) *canadensis calderoni,* Creighton, 1950, p. 276. New synonymy.

Leptothorax yankee var. *kincaidi* Pergande, 1900, Proc. Wash. Acad. Sci., 2: 520, worker, female; *L.* (*M.*) *canadensis kincaidi,* Creighton, 1950, p. 277. New synonymy.

Leptothorax canadensis var. *yankee* Emery, 1895, Zool. Jahrb. Syst., 8: 319, worker; *L.* (*M.*) *canadensis yankee,* Creighton, 1950, p. 277. New synonymy.

Ecology

Of all the ants occurring in North America, *Leptothorax muscorum* is the species best able to survive in extreme Arctic-alpine conditions. Throughout boreal and alpine North America within the limits of the timbered areas, *L. muscorum* is found in company with *Camponotus herculeanus* (Linnaeus) and *Formica neorufibarbis* Emery,[2] the two dominant ants of the region.

[2] *C. herculeanus* has also gone under the varietal name *whymperi* Forel. *F. neorufibarbis* has usually been recorded as *F. fusca* var. *gelida,* and was listed by Brown (1949) and Weber (1950) as *F. fusca.* The subspecies of *neorufibarbis* retained by Creighton appear to be untenable.

On Mt. Washington, New Hampshire, along the toll road on the eastern slope, tree line occurs at about 4000 to 4200 feet altitude. In the interior of the thick, dark spruce forest below 4000 feet, ants are very scarce or absent, probably due to inadequate insolation, but in the low, spaced wind timber (*Picea mariana*) at treeline, nests of *Formica neorufibarbis* are very abundant under stones. In similar nests under stones at this level are also found a few populous nests of *Camponotus herculeanus,* unable to utilize the spindly wind timber for nesting. *Leptothorax muscorum* at this belt is relatively scarce, being found mainly as strays in or near the nests of the two larger species. These three are the only ant species so far taken at or above tree line on Mt. Washington.

Above tree line, up to about 4500 feet on the open tundra-like "lawns," *F. neorufibarbis* continues as a fairly abundant nester under stones. Established nests of *C. herculeanus* here reach only to about 4300 feet. At 4700 feet (Nelson Crag), I found *L. muscorum* suddenly abundant in a strip extending away from the road in both directions, under small, flat stones, fully exposed on the soil surface. These nests, while mostly consisting of the usual 50 to 100 workers, dealate females and intercaste females normal for the species, also harbored in several instances a complement of winged males and females (July 19, 1952) in proof of their flourishing condition. At the same station, intensive search revealed only a single nest of *F. neorufibarbis,* and this in a situation sheltered by a low rock ledge and mat spruce. (*F. neorufibaris* and *L. muscorum* have very recently been taken at over 5000 feet on another slope.)

In northern Alaska, Weber (1950) records a worker of *L. "canadensis"* from Umiat on the Arctic Slope, where it is the only species of ant so far collected. I have published records of all three of the Arctic ants discussed above from the collections of Dr. Marie Hammer at Reindeer Depot in the Mackenzie River Delta, just a few miles from the Arctic Ocean (Brown, 1949; see footnote 2, above). Since that time, I have received more extensive series of the same three species from Dr. W. J. Brown, of the Canadian Department of Agriculture, Division of Entomology.

These series are also chiefly from Reindeer Depot, from the survey collections of Dr. Brown and Mr. J. R. Vockeroth, and they are accompanied by Dr. Brown's notes in a letter, from which I should like to quote, with insertion of my determinations of the ants in brackets.

"Reindeer Depot is on the eastern edge of the Mackenzie Delta at lat. 68°43′, long. 134°06′. It is well treed, but the last species, *Picea glauca* Voss, extends down the river only eight or ten miles. About 200 yards from the river, the Caribou Hills rise very steeply to about 500 feet, to bound the Delta on the east. The upper halves of the protruding parts of the slope are clay and quite bare except for small clumps of grasses, *Hedysarum,* and a few other low plants. The bare parts supported a surprisingly rich fauna, an intrusion from the south, that did not occur elsewhere in the region. [*F. neorufibarbis*] seemed tied to this habitat. The others occurred on the lower slopes, which were mostly sphagnum well covered with trees and other vegetation. Beyond the crest of the Caribou Hills, rolling, treeless tundra extends east and north to the limits of land. This tundra is sphagnum that thawed to a depth of from eleven to nineteen inches in the summer of 1948. It is fairly well covered with low, arctic plants. It was here, beneath firewood left at an old camp site of reindeer herders, that [*L. muscorum*] was taken, about a mile from the trees."

Dr. Brown also sent one worker of *L. muscorum* taken at Kidluit Bay on Richards Island (lat. 69°32′, long. 133°47′) in the Arctic Ocean, about 50 miles airline from any trees. Dr. Brown notes that great quantities of driftwood are found at this locality, however, which might mean that the ant is really not permanently established on Richards Island. It is of interest to note that this seems to be the northernmost record for ants in the Western Hemisphere. Dr. Brown concludes:

"I have not seen other ants from treeless tundra. Lack of trees and consequent exposure to wind causes abrupt, major changes in fauna and other flora. I have believed that ants ended with the trees."

The Mackenzie Delta *muscorum* sample contains a goodly proportion of both concolored and bicolored pigment forms with all possible intergrades, and frequently uninidal.

In Colorado, Gregg (1947) found *L. muscorum* and *F. neorufibarbis* (under the older conventionally used names) to be the "only two species . . . discovered with any regularity" above timber line, and then only on the lowest and best-protected slopes. Eidmann (1933) reported the usual trio of Arctic species from Labrador, from collections made in the region of the Matamek River.

Such records render it very likely that *L. muscorum* inhabits the whole of the spruce-fir forest land of Arctic America and the greater part of the similar vegetational zones in the higher mountains, and that it can also exist in places a bit beyond the limit of trees where conditions are not too extreme. This little species can also occur at slightly greater extremes on the warm side of its range than can either of its two usual companion species, though all of these forms apparently are absent from the spruce and fir forests of the southern Appalachians, where intensive search has been made for them.

At White Lake, Ossipee, New Hampshire, and Saco, Maine, I found slightly dwarfed examples of *muscorum* nesting in a stand of *Pinus rigida* growing on sand; E. O. Wilson took a nest at the top of Snow Bowl Road, San Francisco Mts., Arizona, in pine-aspen to spruce-fir transition.

It would be interesting to see prepared a synthesis of the information available on the Eurasian populations of *muscorum,* but such a work would immediately run afoul of the doubtful identifications abounding in the Old World literature; many of these probably apply to *acervorum* or other species, and *vice versa.*

References

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Useful Information for Field Collectors in Mexico

As a result of the advent in recent years of a tremendous increase in faunal studies in Mexico on the part of biologists from other countries, particularly those from the United States, information on the proper method of obtaining scientific collecting permits and regulations concerning the obligations on the part of the collectors are set forth briefly in the following paragraphs in the hope that they will prove helpful to those contemplating biological investigations in Mexico.

Scientific collecting permits are required of all investigators who contemplate taking insects or other zoological specimens in Mexico. These permits are issued free of charge by the Dirección General Forestal y de Caza of the Secretaría de Agricultura y Ganadería, located at Mariscal Street No. 11, Mexico, D.F. All correspondence concerning scientific collecting permits should be addressed to that office. Any representative of a scientific or cultural institution, including students, who demonstrates qualifications satisfactory to the Mexican Government, is eligible to receive a permit.

Applications should be made at least one month in advance, stating the type of study to be undertaken, the part of Mexico in which the study is to be made and the duration of the field phase of the investigation. A recent photograph of the applicant should accompany the application.

Recipients of scientific collecting permits issued by the Mexican Government are under obligation to fulfill the following requirements as stated on each permit:

a. To return one specimen of each species collected to the Mexican Government (these specimens will be deposited in the collections of the Instituto de Biologia, of the National University of Mexico, or in some other reliable scientific institution).
b. To submit a summary of field observations and a list of specimens collected.
c. To send reprints of publications and reports based on the material gathered in Mexico.

(Obligations a, b, and c were designed to apply to vertebrate animals. In so far as is practicable, the spirit of these obligations should be observed by entomologists also, but we realize that difficulties of identification and the enormous numbers of specimens obtained make compliance in detail difficult or impossible.)

d. To cooperate in game law enforcement by reporting cases of game law violations.
e. To abide by the game laws of Mexico, paying particular attention to the seasonal hunting regulations, and cooperating in giving full protection to those species completely protected from hunting. Permission to take species on the protected list may, in certain cases, be issued at the discretion of the Direccion General Forestal y de Caza.

Specimens, reports, reprints, etc. being submitted in compliance with a to c above should be addressed to Direccion General Forestal y de Caza, Departmento de Caza, Mariscal No. 11, Mexico, D.F.

Authorization for temporary importation of firearms and ammunitions and for carrying firearms in pursuit of scientific studies in Mexico must be obtained in advance from the Departmento de la Industria Militar in every Customhouse along the Mexican–U. S. border, or directly from the central office at Tecamachalco, D.F.

BERNARDO VILLA R.
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Nomenclature Notice

All comments relating to the following should be marked with the file number and sent to Francis Hemming, 28 Park Village East, Regent's Park, London N.W.1, England.

rufa Linnaeus, 1761, as published in the combination *Formica rufa,* proposed validation of, and designation as type species of *Formica* Linnaeus, 1758 (Class Insecta, Order Hymenoptera) (pp. 309–318) (File Z.N. (S.) 224).

Details in *Bull. Zool. Nomencl.* Part 10 of Vol. 9.

Helocordulia uhleri (Selys), a Dragonfly New to Ohio

By Robert A. Champlain and Russell W. Whiting, Department of Zoology and Entomology, Ohio State University, Columbus, Ohio

On 1 May, 1954, a female of this species was captured at Conkle's Hollow, Hocking County, Ohio, by the junior author while it was flying down the center of a woods-bordered road.

On 16 May, 1954, three males were captured at Tar Hollow State Park, Hocking County, Ohio, by the senior author. They were making regular patrols about a foot above the surface of a small rocky brook which was formed by the overflow of a small lake.

This insect has been recorded from Ontario, Maine, New York, Pennsylvania, Connecticut, New Jersey, North Carolina, and Kentucky. Wright [1] has recorded its occurrence in Alabama, Tennessee, and Louisiana, but his identification is based upon the nymph. The Ohio captures described above represent the westernmost record based upon adult characters, and they constitute a new state record. This brings the total number of species of Odonata recorded from Ohio to 139.

All specimens were identified by Dr. D. J. Borror of this department. Two of the males and the female are in the collection of Dr. Borror, while one male remains in the collection of the senior author.

Reviews

The Physiology of Insect Metamorphosis. By V. B. Wigglesworth (Univ. Cambridge). Pp. viii + 154, 45 figs. Cambridge Monographs in Experimental Biology. Vol. 1. Cambridge University Press. (American Branch, 32 E. 57th St., New York 22.) Price, $2.50.

The greater portion of this book is devoted to the endocrinology of growth, moulting, and metamorphosis. It presents this

[1] Wright, M. 1946. Ohio Jour. Sci., 46: 337–339.

subject as it has developed, beginning with the work of Kopeč, in 1917, and continuing down to the isolation and chemical analysis of the thoracic gland hormone in 1954. Compared with earlier reviews of the subject by other authors, this is truly a masterly work, distinguished by its comprehensive approach and the fact that this author has taken the trouble to ensure that every detail, as well as the argument as a whole, will be absolutely clear to the reader. The writing is so concise that it requires attentive reading, yet care is taken to emphasize the important points by recapitulation.

But this book is definitely more than a recital of past researches, it is a serious attempt to arrive at a real understanding of the mechanism of metamorphosis and to relate it to the problem of polymorphism and to the broader problems of development and differentiation as they have interested modern geneticists, experimental embryologists, endocrinologists and cellular physiologists.

As regards metamorphosis, that of the hemimetabola is made the primary basis of discussion (although all significant work on the holometabola is also drawn in), not so much because the author's own work was on *Rhodnius,* but because in this group the alternative laying down of now larval, now imaginal structures in the body surface by the self-same cells can be best studied. It becomes evident that the larval epidermis contains, invisibly, a latent imago, and the imago, indeed, still retains the larval pattern, latent but exposable in the partial reversal of metamorphosis obtained as the result of experimentally induced post-adult moults. Polymorphism, likewise, depends upon such a dual or multiple potentiality; in fact metamorphosis is but a special type of polymorphism, in which the potential types of differentiation appear sequentially in the same individual. Furthermore, the fact that in every insect the various body regions produce different structures (legs, antennae, etc.), is again an instance of genetically uniform tissues having a multiple potentiality. We thus come to realize that metamorphosis is a problem that is not fundamentally different from the general problem of growth and differentiation in organisms in general.

In the last chapter ("Differentiation and polymorphism"), the broader problems of differentiation are then taken up: integration of growth, relative growth rates of different parts, the nature of the substrate, homeosis, and polymorphism. Wigglesworth describes in detail the sensory bristles in the epidermis of Rhodnius and their increase in numbers at each moult. As existing bristles, with their plaques, come to lie farther apart, new ones are induced at fixed distances from the existing ones.

A given cell, it is thought, absorbs the plaque-forming substance (produced locally) and becomes the center for a new plaque that drains this substance from the surrounding area, so that other cells in the area are prevented from forming plaques.

In the induction or evocation of the larger organs also, and in the production of polymorphic forms, and in metamorphosis, similar phenomena are responsible. The modifying substances may be of local origin, they may be produced by endocrine glands, by other glands (as for "social" hormones), or even be found in the food. It is the concentration of these substances (for they are used quantitatively by the cells and are not merely triggering), and their timing that are significant, as well as the substrate. The nature of the modification is also considered, whether acting on plasmagenes, altering the cytochrome system, other enzymes, etc.

Thus entomologists experimenting on insect development are contributing to the solution of the same fundamental problems that are occupying leading experimental biologists in other fields. The interpretation of differentiation as presented (based on the ideas of Wigglesworth and others who are mentioned) is not claimed to be more than a "rather schematic model of the process actually occurring. . . . But a hypothesis which provides a consistent description of the facts, and can be used to predict the changes that occur is not without value."—R. G. SCHMIEDER.

DIE SCHMETTERLINGE MITTELEUROPAS. By Walter Forster and Theodore A. Wohlfahrt. Bd. I/II, Lfg. 3, 4, 5, 12 pls. Franckh'sche Verlagshandlung. W. Keller & Co., Stuttgart, Germany. Vol. I, now complete, bound in linen, DM 23.

The appearance of the first Lieferung of this beautiful new work was noted in ENT. NEWS for July 1952. The three parts now in hand complete Volume I and parts of Volume II of the mid-European butterflies. Volume I comprises 202 pages and deals with the biology of the butterflies. The first 60 pages are on collecting and breeding, and on the preservation of all stages in collections. Then follow chapters on anatomy, development, color and color patterns, ecology, parasites and diseases, geographical distribution, the genetics of butterflies, nomenclature and systematics, and evolution.

Of Volume II, 12 of the color plates and some text pages were included in these Lieferungen; and it will be completed with the appearance of Lfg. 6, expected soon.—R. G. SCHMIEDER.

EXCHANGES

This column is intended only for wants and exchanges, not for advertisements of goods for sale or services rendered. Notices not exceeding three lines free to subscribers.

These notices are continued as long as our limited space will allow; the new ones are added at the end of the column, and, only when necessary those at the top (being longest in) are discontinued.

Cynipid and Itonidid galls—American species wanted; purchase or exchange for British species. Fresh or dried. D. Leatherdale, F.R.E.S., Old Woodstock, Oxford, England.

Wanted—Reprints or papers concerning insects taken in Alaska for inclusion in list of Alaskan insects. R. H. Washburn, Alaska Experiment Station, Palmer, Alaska.

Conopidae of the World wanted. Will pay 10¢ to $1.00 for pinned and labelled specimens. S. Camras, 4407 N. Milwaukee Ave., Chicago 30, Illinois.

Anisoptera—Nearctic sp. wanted for exchange, espec. Ophiog., Arigom., Aeschna, Neurocor., Somatoc., Cordulia, Dorocor., Leucor. R. D. Cuyler, Dept. of Entomology, N. C. State College, Raleigh, N. C.

Bembicini and Stizini (Hym., Sphec.) of New World wanted for revis. study. Will return upon request or at end of project. James E. Gillaspy, Dept. of Zoology, Univ. Texas, Austin 12, Texas.

Agapema galbina. Will exchange cocoons of this moth for nature books. E. Frizzell, Route 4, Box 96, San Benito, Texas.

Wanted—Data on exact location of colonies of *Epibembex* (olim *Bembix*) (Hymenoptera), any species, any part of country, for biological studies. Howard E. Evans, Dept. Entomology, Cornell Univ., Ithaca, N. Y.

Fanniinae wanted on loan (nearctic and holarctic), and information on collections. James G. Chillcott, Dept. Entom., Univ. of Kansas, Lawrence, Kan. (Loans may be charged to Dr. C. D. Michener.)

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